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Global warming may depress avian population fecundity by selecting against early-breeding, high-quality individuals in northern populations of single-brooded, long-lived species

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Global climate is changing at an unprecedented rate. Adjustments to breeding phenology represent responses to current climate change, and some climatic effects have negatively affected population reproductive performances. Here we simulated the possibility that climate warming-induced changes in the timing of egg-laying may modify the phenotype composition (i.e. proportion of high- *vs*. low-quality phenotypes) of avian populations of single-brooded, long-lived species in northern countries (where asymmetric changes of weather conditions are more pronounced), therefore affecting the internal structure and long-term stability of populations. In northern countries, pre-laying temperatures have risen and laying and hatching are expected to occur earlier. However, because post-hatching temperatures have remained stable, early chicks hatch under conditions of low temperature and great precipitation, and may face increased mortality. Because early breeders are generally high-quality individuals, their contribution to the future recruitment of the breeding population will decrease, engendering a doubly negative effect: (1) the number of offspring in a population will be lower than in the past because of higher mortality in the largest broods; and (2) the population will increasingly be composed of the offspring of low-quality individuals, which will consequently decrease fitness of the entire population.

Introduction

Global climate is changing at an unprecedented rate (Parker *et al*. 1994, Pachauri & Reisinge 2007) and because current trends in climate change are expected to accelerate in the near future, we face the urgent challenge of predicting the responses of life forms under future climatic

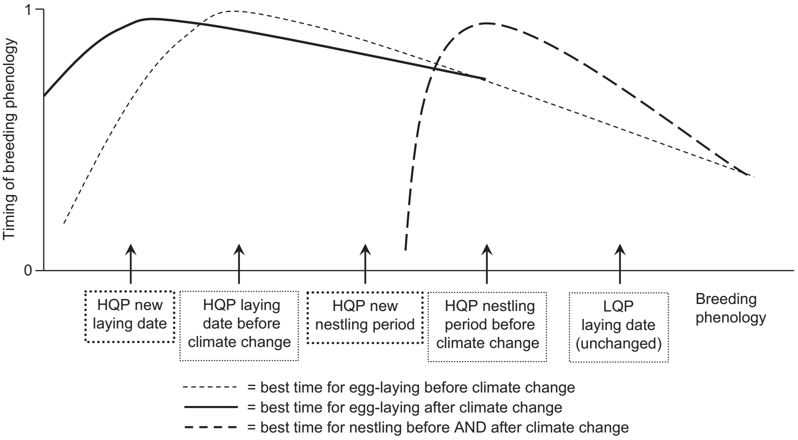

Fig. 1. The new breeding scenario caused by global warming. As a consequence of altered weather conditions during the early breeding period, pre-laying temperatures have increased but post-hatching temperatures have remained stable. In the interval since the onset of asymmetric climate change, the timing of laying and hatching by early breeders (i.e., with high-quality phenotypes, HQP) has advanced, shifting from the dashed to the thick line. Consequently, present post-hatching rearing conditions for the offspring of high-quality breeders (thick dashed line) are worse than in the past, with lower temperatures and increased precipitation. A direct consequence is that chicks hatching into these lower temperature/higher rainfall conditions face greater mortality, and the breeding success of early breeders is thus lower than it was several decades ago. This will lead to a reduction in the contribution of high-quality phenotypes to the population, because their offspring are likely to be subject to the highest mortality rates. In contrast, the chicks of later breeders (i.e., with low-quality phenotypes, LQP) will hatch under unchanged breeding conditions, and, consequently, the contribution of low-quality phenotypes to the population is expected to remain similar to that in the past.

scenarios (Dunn 2004, Sekercioglu *et al.* 2008, Visser *et al.* 2009).

Among the effects of new climatic conditions on vertebrates, the consequences of global warming on the timing of bird breeding have been well documented (Dunn 2004, Leech & Crick 2007, Both *et al.* 2009, Lehikoinen *et al.* 2009, Visser *et al.* 2009, Schaper *et al.* 2012). Previous studies have reported that, in most cases, the trend to lay eggs earlier represents a response to climate change (i.e. individual adjustments to increasing temperature; Both *et al.* 2004, Pulido & Berthold 2004, Visser *et al.* 2009). The lack of (sufficient) adjustments to breeding phenology frequently has severe negative effects on reproductive performance, size and dynamics of breeding populations. This is mainly attributable to the mistiming between periods of egg laying and (a) optimal food supply during the nestling period (Sæther *et al.* 2004, Visser *et al.* 2004, Both *et al.* 2009), and/or (b) the best conditions for the rearing of offspring (Ludwig *et al.* 2006, Lehikoinen *et al.* 2009).

However, it may be that the more immediate, evident and easily detectable warning signs of a changing global condition (e.g. decreased fecundity and population numbers, reducing recruitment into the breeding population) could mask a more subtle and unrecognized malaise among several avian populations with specific life-history traits. Here we present a mathematical model to explore the possibility that climate warming-induced changes in the timing of egg-laying may modify the phenotype composition of the entire avian population (i.e. proportion of high- *vs.* low-quality phenotypes), therefore affecting both its internal structure and long-term stability.

The logic of this potentially overlooked process is the following (Fig. 1). In northern countries, weather conditions during the breeding period have changed because of warming. Pre-laying temperatures have increased (Houghton *et al.* 2001), and, consequently, both laying and hatching are expected to occur earlier (i.e. breeding onset is earlier) since temperature directly affects the timing of breeding (Visser *et al.* 2009). However, because post-hatching temperatures have remained stable, temperatures during the brood-rearing period have decreased because of the earlier onset of breeding (Lehikoinen *et al.*

2009). Thus, as late spring temperatures have not correspondingly increased (i.e. climate change is asymmetric), chicks hatching under conditions of lower temperature and greater precipitation may face increased mortality. This means that post-hatching conditions are now worse in general than in the past. Therefore, the breeding success of early breeders is expected to be lower than it was several decades ago because chicks die as a consequence of severe weather conditions. Although researches have been able to show this effect only recently (Ludwig *et al*. 2006, Leech & Crick 2007, Lehikoinen *et al*. 2009), and it seems that it mainly acts on species with similar breeding phenology (i.e. single-brooded, long-lived species), we have to take into consideration that: (i) field results showing the effect of climate change are still relatively scarce and mainly focused on the same groups of species (i.e. passerines), despite the fact that different species may experience different constraints and scenarios. In fact, the large number of species (and consequent different life-histories) and their sometimes wide distribution may engender dissimilar patterns under the same climatic constraints (e.g. depending on local conditions the effect of climate change might act differently on the same species); and (ii) two of the species for which such an effect has been recorded, the black grouse *Tetrao tetrix* (Ludwig *et al*. 2006) and the common buzzard *Buteo buteo* (Lehikoinen *et al*. 2009), share several peculiar features with many other species, e.g. low population densities and a conservation concern status. Consequently, the above-mentioned points might indicate that such a scenario could be more widespread than is currently realised.

Among migratory species it is well known that high quality individuals (i.e. individuals in good physiological condition that can afford migration costs earlier in the season; high-quality phenotypes, HQPs) arrive early at the breeding grounds and occupy the best breeding sites, and will therefore reproduce earlier and more effectively (Forstmeier 2002, Bêty *et al*. 2004, Ninni *et al*. 2004, Vähätalo *et al*. 2004, Rainio *et al*. 2006, Pulido 2007, Sergio *et al*. 2007, Møller 2008, Both *et al*. 2009). Among resident species, HQPs generally start breeding earlier than do low-quality phenotype (LQP) individuals, mainly because the former are owners of the best nesting sites (i.e. breeding places with the best cover and food availability). Such HQPs are generally expected to contribute more to future recruitment of the breeding population (Klomp 1970, Daan & Tinbergen 1997) than LQP individuals. However, because of climate warming, early breeders of those species whose breeding success is affected by ambient weather conditions will face a bottleneck of worsening post-hatching conditions (Lehikoinen *et al*. 2009) and, consequently, the contribution of HQPs to a population will decline because their offspring may incur the highest mortality rates. In contrast, chicks of LQPs will hatch under unchanged breeding conditions because of the asymmetric effect of climate change during spring, and, consequently, the proportional contribution of LQP chicks to the population will be greater than in the past. This scenario has the potential to have a negative effect. First, in general the number of offspring in a population will be lower than in the past because of higher mortality in the largest broods (those of the HQP individuals), and second, the population will increasingly be composed of the offspring of LQPs, which will consequently decrease its fitness.

Methods

Main assumptions behind the modelling approach

Our modelled scenarios (the models were implemented in MatLab) describe a population containing n breeders of both LQP and HQP, with different annual mortality rates. We assumed a very conservative starting scenario involving a population composed of 70% of HQP and 30% of LQP. Each pair produces a density-dependent number of offspring but, because of their better physical condition, the breeding output of HQPs is higher than that of LQPs. We assumed that HQP nestlings' mortality rate under the effects of climate change is higher than the mortality rate under unchanged breeding conditions, i.e. before global warming conditions. To explore the potential effects of climate change under varying conditions of HQP nestling mortality, we decided to consider four representative scenarios with differing values of HQP nestling mortality, representing low to severe effect of global warming: (1) scenario 0: 10%, corresponding to half of LQP nestling mortality (*see* below), i.e. HQP nestlings are supposed to survive more than LQP ones because of the better phenotype of their parents; this scenario simulates a population trend when climate change is not acting; (2) scenario 1: 50%, to simulate a mild effect of climate change; (3) scenario 2: 75% for an intermediate effect; and (4) scenario 3: 95% for the worst climate change scenario. Since LQP nestlings faced unchanged breeding conditions, we assigned them a constant mortality rate (*see* section 'The Model' below). This ecological setting allows us to investigate trends in population phenotype composition under different conditions of climate warming. Both HQP and LQP juveniles have a mortality cost during dispersal, such that some emigrants die. All surviving individuals were potential partners in the next generation, and were included in the list to make up a new pair with unmated breeders (those pairs that have lost a mate due to breeder mortality). HQP and LQP individuals were randomly coupled (i.e. independent of its quality), and HQP individuals were coupled before LQP to follow main temporal patterns of mating in bird populations (i.e. good breeders reproduce before poor ones). When a pair was formed by two HQP individuals, it was considered a HQP pair, whereas when the pair was made up by two LQP individuals it was considered a LQP pair; a pair formed by a HQP and a LQP individual will have chicks whose quality is randomly selected from a uniform distribution of mean = 1. This also prevent that the LQP or HQP phenotype would become artificially dominant in the population. The model considered a population with a large number of individuals (n = 1000), for which we ran 100 simulations of 100 years for each scenario.

The values related to mortality, fecundity, survival and pairing of our modelled population (*see* below) are similar to the ones previously used to simulate a population of a single-brooded, long-lived species (Penteriani *et al.* 2006), i.e. a population with characteristics of the species for which such a new breeding scenario has been recorded in the field.

Although we are aware that (a) individual quality is a simplistic way to define complex inter-individual differences in traits associated with survival and reproduction (Wilson & Nussey 2009), and (b) the concept of individual quality may show quite a wide gradient of variation within the same population, we considered that the separation of individuals into 'high' and 'low' quality is appropriate here because it is strictly related to the concept of the narrow temporal window during which reproduction is better, and which mainly allows for early (HQP) or late (LQP) breeding.

The model

Following Penteriani *et al.* (2006), the dynamics of the population was simulated by individual-based evaluations of the following three stochastic functions.

Function 1: death

The death of an individual depends on its quality (HQP or LQP) and on its social status (breeder or dispersing). An individual will die if;

$$r < A(a) + [1 - A(a)]B(s) \qquad (1)$$

where r ($0 < r < 1$) is a uniformly distributed random deviate, a is the condition of the individual and s its social status. $A(a)$ and $B(s)$ are randomized discrete functions that describe the probability of death as a function of the quality and the status of the individual, respectively;

$$A(a) = knP(a) \qquad (2)$$

$$B(s) = knP(s) \qquad (3)$$

where k (fixed for each year, representing environmental stochasticity) and n represent normally distributed random variates with mean 1.0 and standard deviation 1.0. $P(a)$ is a discrete function returning 0.15 for HQP and 0.20 for LQP, and $P(s)$ is a discrete function returning 0.10 for breeder and 0.30 for dispersing. Equation 1 implements the logic for the two probability distributions.

Function 2: breed and chick survival (i.e., effects of a warming climate)

Fecundity is modelled as density dependent, relying on the levels of population saturation. Therefore, this function returns the number of chicks produced during the current year as a density-dependent distribution;

$$N(c) = w(c)D_h + [1 - w(c)]D_1 \quad (4)$$

where c is the number of breeding pairs and w is a weighting term for the two discrete fecundity functions D_h and D_1

$$w(c) = (c/\text{cap}/2)^{10} \quad (5)$$

This value represents the "saturation" of the population, where c is the number of breeding pairs and cap represents the population capacity (in our case cap = 1000 individuals). D_h is the high limit of the percent point function (PPF) of the discrete fecundity distribution E_h that describes the probability of raising a given number of chicks for a population saturation threshold = 1 (i.e. the population is completely saturated; Table 1).

D_1 represents the low limit of the fecundity distribution of PPF of the discrete fecundity distribution E_1 that describes the probability of raising a given number of chicks for a population saturation threshold = 0 (population completely unsaturated; Table 2).

We assumed that each pair, independently of its quality, produces chicks of both high and low quality, but with different probabilities, the probability for a chick to acquire the same phenotype of its parents being higher. Thus (i) a HQP pair produces a HQP or a LQP chick with a probability of 0.8 or 0.2, respectively; (ii) the probability that a LQP pair has a LQP or HQP chick is of 0.8 or 0.2, respectively; and (iii) a mixed HQP-LQP pair produces a HQP or a LQP chick with a probability of 0.5. Nestlings have a probability to die giving by the following function;

$$C(c) = knP(c) \quad (6)$$

where k (fixed for each year, representing environmental stochasticity) and n represent normally distributed random variates with mean = 1.0 and standard deviation = 1.0. This probability is higher for HQP chicks due to the effect of warming. $P(c)$ is a discrete function returning a constant value of 0.2 for LQP chicks and 0.50 (scenario 1), 0.75 (scenario 2) and 0.95 (scenario 3) for HQP chicks. Only the chicks that survive will be listed in the next generation as juveniles and follow the different rules.

Table 1. Probabilities of raising a given number of chicks for a population saturation threshold = 1 (i.e. population completely saturated), for both high-quality (HQP) and low-quality (LQP) phenotypes.

Number of chicks[a]	HQP	LQP
0	0.03	0.10
1	0.22	0.40
2	0.40	0.30
3	0.35	0.20
4	0	0

[a] The number of chicks is selected as the value of the percent point function for an uniformly distributed random variable.

Function 3: couple

This computes a suitable partner for the current individual. All dispersing individuals are potential partners and included in a list to couple with unmated breeders (those pairs that have lost a

Table 2. Probabilities of raising a given number of chicks for a population saturation threshold = 0 (i.e. population completely unsaturated), for both high-quality (HQP) and low-quality (LQP) phenotypes.

Number of chicks[a]	HQP	LQP
0	0	0
1	0.05	0.30
2	0.35	0.35
3	0.35	0.30
4	0.25	0.05

[a] The number of chicks is selected as the value of the percent point function for a uniformly distributed random variable. For intermediate values of saturation, the probability is calculated as weighted average of the extreme values: saturation × productivity(1) + (1 – saturation) × productivity(0).

mate due to breeder mortality). HQP and LQP individuals can be coupled randomly (i.e. independently of its quality). Each candidate in the population is tested and coupled with a density-dependent probability function,

$$C(c) = 1 - w(c), \qquad (7)$$

of the number of couples c in the population. If a partner is eventually found, both the individual being evaluated and the chosen partner are considered in the next generation as a breeder (a pair). As explained above, among dispersers HQP individuals are evaluated before LQP ones.

During each cycle (year) the following events took place in the subsequent order: (1) deaths of adults (for simplicity, we assumed that the death of a breeding individual implies that it does not produce any chick); (2) breeding of those pairs in which the female and male survived; as a consequence of reproduction, each breeding event results in a (density-dependent) number of chicks, which will survive or die. Survived chicks have a quality status of HQP or LQP and become adults; and finally (3) mating.

Results and discussion

In the modelled population in which 70% of the breeders were initially HQP individuals, offspring mortality caused by global warming had the potential to rapidly and dramatically change breeder phenotype frequencies (Fig. 2). The originally dominant HQPs dramatically decreased after a few dozen years under the intermediate climate change scenario, and approached extinction after ~100 years under the worst climate change scenario, being composed mainly of LQPs at the end of the simulation. Population size also decreased (Fig. 2A) because of both the decrease of HQP individuals and the higher proportion of substandard LQP individuals with lower breeding performance (Fig. 2B and C). This performance is not affected by climate change as asymmetric changes do not alter the quality of the temporal bracket of the LQP breeding phenology. Results for the intermediate and worst climate change scenarios predict that the population would be reduced to approximately one-third of the starting population in less than 50 years. Both the decrease in size of the breeding population and the alteration of the phenotypic structure, i.e. the population ends to be quite exclusively composed of substandard breeders, have the potential to increase the extinction risk of the population under any event of demographic and/or environmental stochasticity. However, it is important to highlight that because of the unknown circumstances populations could face under these new and never before experienced breeding conditions, some events may alter the scenario revealed by our simulation. Firstly, although our model takes into account a possible compensatory mechanism as density-dependent effect on fecundity, it does not consider the eventual possibility that LQPs would be able to breed in the higher-quality territories of HQPs, which could reduce the negative effects of climate warming on the population. We are tempted to suppose that, once climate change causes offspring from HQP parents to die in greater numbers (because they are born earlier in the season than optimal), offspring from LQP parents can then occupy the vacant, high quality habitats. This means they would end up in better physiological condition, and hence have higher survival, fecundity and so on. However, if LQP breeders are be able to shift to a high quality status, they will consequently behave as HQP, i.e. they will start to breed earlier, when conditions are not optimal. Under this assumption, climate warming may also be acting as a kind of evolutionary trap (i.e., maladaptive behavioural or life-history choices made despite the availability of higher-quality options; Schlaepfer *et al.* 2002) later in time, when a reduction in high-quality breeders will allow low-quality breeders to move to better habitats and, as an end consequence, will continue the cyclical chain of events that lead to the population decrease. Finally, we cannot discard the possibility that LQP could also shift their breeding date if conditions improve early in the season. However, this possibility seems quite remote for both migratory and resident species because: (a) low-quality migrants are always expected to arrive later to the breeding grounds than high-quality individuals (their physiological condition being unrelated to the climatic events of the

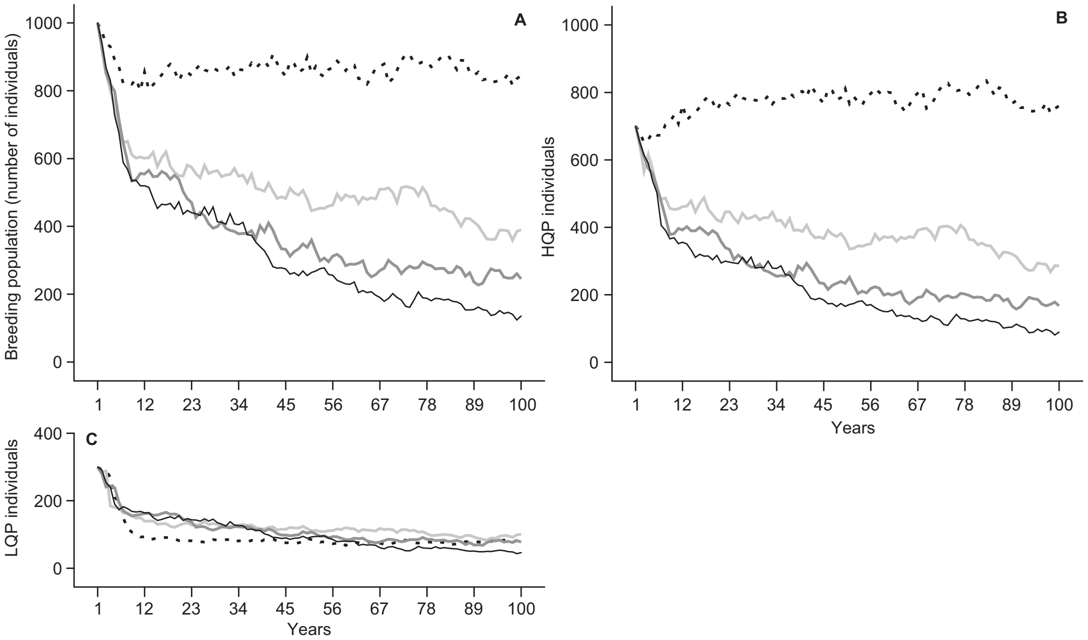

Fig. 2. The new breeding scenario engendered by climate warming has the potential to have a double negative effect on the breeding population (**A**) a combination of plots **B** and **C**, meaning all individuals in the simulated population), high-quality phenotypes (**B**) and low-quality phenotypes (**C**). First, the population will increasingly be composed of low-quality phenotypes and, second, population size will decrease because the number of offspring will decline as a result of higher mortality in the largest broods (those of the high-quality early breeders). We represent here the effects of three scenarios with different values of chick mortality under the effects of climate change (*see* text for details) on a starting population of 1000 individuals, composed of high-quality (HQP) and low-quality phenotype (LQP) individuals in a conservative proportion of 70% and 30%, respectively. Averages for 100 simulations of 100 years for each scenario are shown as black dots for the scenario without climate change, light grey lines for the mild scenario (50% of chick mortality), dark grey lines for the intermediate scenario (75% of chick mortality) and black lines for the worst scenario (95% of chick mortality). The sudden fluctuation immediately after the start of the simulations is an artefact owing to the unavoidable misfit between the initial fixed structure imposed to the population and its equilibrium structure, which depends on the simulation dynamics (*see* Penteriani *et al.* 2005 for more details).

breeding areas), also considering that migratory birds seem to be unable to adjust migration phenology so as to keep track the advancement of spring at their breeding grounds (Saino *et al*. 2010); and (b) resident LQP are expected to occupy substandard areas and, consequently, it does not seem probable that they can easily afford the costs of early reproduction.

It seems that climate change may have disturbed the previous fragile cycle of strictly related effects and consequences, wherein birds born early in the season and raised in the best territories (i) fledged under the best conditions, (ii) commenced dispersal with the highest probability of survival, (iii) were likely to occupy the best habitats in winter (thus ensuring the maintenance of good individual condition and early return to the breeding sites), which ultimately (iv) enabled such individuals to contribute disproportionately to subsequent generations (Lack 1968).

The timing of reproduction is a life history factor with crucial fitness consequences and for many species there is a relatively brief period in the year when conditions are favourable (especially in northern countries). Reproduction decisions are influenced by both environmental conditions (e.g. food availability and weather) and the intrinsic properties of individuals (e.g. body size and foraging efficiency). Modifying climate confuses breeders because their life-history traits, which should follow an optimal reaction norm with respect to the encountered conditions (Bêty *et al*. 2004), trap them in the wrong reproduction time bracket. Prior to climate warming the seasonal decline in avian fecundity generally showed a seasonal decline in offspring survival (i.e. later breeders reproduced less effectively). However, climate change has opened a new temporal window, creating conditions that trigger reproduction but are ultimately detrimental to offspring survival, thus confounding the fine-tuned cues by which breeders have always made their reproductive decisions.

With the discovery of a generalized trend towards earlier reproduction, it was hypothesized that higher temperatures could lead to greater production of young, simply because earlier laying is usually associated with larger clutch sizes and more fledglings. However, it is now clear that warmer spring temperatures may locally lead to a mismatch in the timing of egg-laying relative to rearing conditions, and there is new evidence for this kind of effect (Ludwig *et al*. 2006, Lehikoinen *et al*. 2009). But, on the basis of the knowledge we currently have on the asymmetric changes in weather conditions that affect mostly northern countries, it is difficult to say if the scenarios we propose represent (i) a relatively rare situation, likely to be applicable to only a few species, or (ii) it is likely to be more widespread across species. Although our knowledge of the complexity of global warming and the potential effects thereof on bird populations is growing, it is evident that our understanding is far from complete.

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